EFFECTS OF ARIDITY ON PLANT DIVERSITY IN THE NORTHERN CHILEAN ANDES: RESULTS OF A NATURAL EXPERIMENT[1]

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ABSTRACT

Hyperarid climates in western South America from 15°S to 29°S, extending up to 3,000 m in the northern Chilean Andes, result primarily from the Andes intercepting precipitation from the Intertropical Convergence and the drying effect of the equatorward-running Humboldt Current bathing much of the Pacific coast of South America. Paleobotanical, paleontological, and geological evidence suggests that such harsh climatic conditions developed very recently in Holocene times, following a turbulent Pleistocene history of alternating wet/cold and warm/dry periods. Seasonal climates probably first emerged in the Pliocene after a long, warm/wet Miocene during which precipitation is thought to have increased from east to west, as opposed to west to east, as occurs north of 25°S today. For the three remaining intact vegetation belts (desert scrub, Andean, and high Andean) in the northern Chilean Andes above the Atacama Desert, surveys on six transects, each approximately one-fourth of a degree latitude wide, located at 18°S, 19°S, 21°S, 24°S, 26°S, 28°S, revealed only 769 species of vascular plants in 290 genera. Altitudinally, species richness decreases with elevation in the winter rainfall zone, where precipitation is received from the southwest ("invierno chileno"; transects 26°S, 28°S), to peak at mid elevations in the summer rainfall zone where precipitation is received from the east ("invierno boliviano"; transects 18°S, 19°S, 21°S, 24°S). Species richness decreases by 80% and cover by 50% over the very severe rainfall gradient from 18–24°S. In spite of its greater reliance on water, the azonal bog flora has been less affected than the zonal flora by aridity, probably because of greater chances of reintroduction of species following their loss through long-distance dispersal. Species richness, when considered on a broad biogeographical scale, was significantly positively correlated with mean annual rainfall, as it was for most 500-m elevational levels when considered separately. The effect of cold temperatures at the higher elevations was completely obliterated by aridity on a biogeographical scale. Although diversity (measured as a synthetic characteristic combining richness and abundance) and species richness showed similar trends as aridity increases, loss of diversity tended to be more gradual in comparison with reductions in species richness. Aridity leads to community features analogous to those seen in the early stages of primary succession, maintained on a permanent basis. Losses in species richness with aridity along the western side of the Andes and from east to west across the Andes were overlain by highly characteristic life form tendencies. Perennial herbs are proportionately most abundant in areas of highest rainfall, annual herbs gain greatest prominence in areas of intermediate aridity, while woody species were proportionately most strongly represented under extreme dry/warm and extreme dry/cold conditions. The woody habit is generally more common in the northern Andes than in some similar North American plant communities. The maintenance of considerable diversity (in spite of severe loss in species richness) coupled with emphasis on long-lived woody species in the harshest environments in the northern Chilean Andes are tendencies also seen in many species-rich, climatically benign tropical plant communities. The hypothesis is developed that convergence in these features results from the similar selective effects of certain abiotic and biotic factors in the harsh arid environments of the northern Chilean Andes and in species-rich tropical communities, respectively. We predict that additional life-history trait similarities (e.g., in breeding systems) will emerge for the plant species of abiotically and biotically "harsh" environments, respectively.

Areas of the earth's surface where local mountain ranges exert strong influence over precipitation and temperature patterns experience especially radical environmental alterations during major global climatic changes. How floras adjust to rapidly emerging harsh environmental conditions, and the patterns of species richness and community diversity resulting from such restructuring should be just as relevant for the development of comprehensive diversity theory as phenomena seen in highly productive, abiotically benign environments. Diversity trends in harsh habitats should also have direct bearing for conservation in that changes induced in ecosystems by human activities are frequently similar in nature and magnitude to those engendered by natural climatic change. Yet, as perusal of the literature on species diversity and community structure (e.g., Tilman, 1986) will show, harsh habitats have received relatively little attention.

Apriorily, reductions in species richness are expected in harsh habitats because productivity is limited by abiotic factors. Such losses, moreover, might be exponential due to the compound direct (physiological) and indirect (historical and, on other organisms such as pollinators, seed dispersal agents) effects of habitat harshness. Patterns of species loss in harsh habitats, nevertheless, are likely to be far more complex than this. Expected losses could be mitigated by a number of factors related to community dynamics. During their evolutionary histories, floras accumulate many life forms varying in ecophysiological and demographic properties. At the onset of harsh conditions, loss of richness could be suppressed by life-form shuffling. In many warm deserts, for example, the annual habit is selectively favored (Raven & Axelrod, 1978; Pavlik, 1985), and species richness levels may be relatively high. Much present knowledge of life form shifts derives from comparative studies of distinct plant communities with floras of heterogeneous phytogeographic origin. Because such comparisons could be confounded by phylogenetic constraints in certain taxa, a critical assessment as to whether life form shifts stall losses in diversity will be best

obtained by comparing life forms in floristically homogeneous communities subject *internally* to different degrees of habitat harshness. To facilitate the interpretation of results, moreover, such gradients in habitat harshness must be well documented as to their abiotic characteristics.

Maintenance of diversity in harsh environments should also be affected by changes in the relative balance of biotic and abiotic selective factors. In early successional communities, because of low dominance levels, local diversity may be high despite total low numbers of species present (Houssard et al., 1980). In that resources are severely limited, and competition for light is reduced due to abiotically induced low productivity, harsh habitats may be likened to the early stages of primary succession maintained on a long-term basis. For harsh habitats with low species richness, then, diversity as reflected in the relative abundance of species might be relatively high. Another way of viewing this postulated analogy is that loss of diversity with greater harshness should be partially, and increasingly, counteracted as harshness increases. This hypothesis may be tested by comparing species numbers (species richness) with measurements of diversity as a synthetic characteristic combining richness and abundance, following Whittaker (1972).

The objectives of this paper are, first, to assess how plant species richness, life forms, and community diversity patterns are affected by severe aridity, and, second, to discuss some implications of diversity patterns in harsh habitats for community structure in general. The northern Chilean Andes located at 18°–28°S in western South America provide a unique setting for this. Close to 10 degrees latitude of absolute desert at low elevations gives way to a sequence of three high-elevation vegetation belts (desert scrub, Andean, and high Andean), these exhibiting varying degrees of aridity latitudinally and altitudinally. Because aridity gradients are overlain by temperature variation, the Andean system is also ideal for assessing the relative effects of temperature versus aridity on plant diversity.

As Diamond (1986) pointed out, to inter-

pret the results of any "natural experiment," as the above would be classed, clear understanding of the timing of historical events that led to the "observed results" is essential. As we mentioned above, the identification of salient present-day abiotic parameters responsible for maintaining the "particular species mix in the test tube" is equally important if unequivocal answers to the kinds of theoretical questions outlined earlier are sought. Consequently, before examining plant diversity patterns in the northern Andes (Section III), we will devote considerable space to outlining the present climatic characteristics of the northern Andes (Section I), and the historical development of arid climates at subtropical latitudes in western South America in general will be reviewed in detail (Section II).

Data Base and Methods

For species richness patterns and estimates of diversity we compiled data over a number of years in six altitudinal transects (18°S, 19°S, 21°S, 24°S, 26°S, 28°S) running from the upper margin of the Atacama Desert (1,500–3,000 m elevation) to the upper limit for vascular plants (4,500–5,000 m, depending on latitude) (Fig. 1). Records of species present every 50 or 100 m of elevation were obtained by walking the transects and by climbing a number of high summits in each area. The transects followed the main Andean penetration routes and for this reason had no fixed courses. In each case routes taken traversed approximately one-fourth of a degree of latitude. For these transects plant cover was measured in altogether 1,620 minimum area quadrats. Replicate quadrats were sampled at 50–100 m elevational intervals along each transect. Cover of shrub and perennial herb species was estimated from the surface area projected by each individual of a species within a quadrat. The largest and smallest diameter of the individual's crown was measured for calculation of an elliptic to circular area. Annual herb cover was initially measured on a phytosociological scale (transects 18°S and 19°S). In later work annual herb cover was estimated from the percentage of

points 10 cm apart on line transects intercepted. The data for all 50–100 m elevational sampling intervals was subsequently pooled for 500–1,000 m elevational intervals.

Species richness for equivalent 500 m elevational intervals at different latitudes was compared with mean annual precipitation using regression analysis, employing linear, semilogarithmic and log–log models, and with mean annual precipitation and mean annual temperature using multiple regression analysis. Precipitation and temperature for the series of 500 m elevational levels on each transect were estimated from curves constructed from weather station data available for the particular area under consideration. Weather data were obtained from di Castri & Hajek (1976) and from records supplied by the Ministerio de Obras Publicas (MOP) in Santiago.

For life form analyses, species were classed as annual herbs, perennial herbs, and woody plants (primarily shrubs). For the small number of Cactaceae present, columnar species and large cushion species were included in the woody category. The smaller cacti species were categorized as perennial herbs. To facilitate statistical analysis (G-tests) the life form data for pairs of adjacent transects were combined.

The indices exp H' where

$$H' = -\sum_i p_i \ln p_i,$$

and $1/\lambda$ where $\lambda = p_i^2$ (Peet, 1974), were employed to measure community diversity. In these indices p_i = the proportional abundance of the ith species. Relative cover was used as the proportional abundance of a species. Details on some of these transects appear in Arroyo et al. (1982, 1984) and in Villagrán et al. (1982, 1983).

I: Present-Day Climates in the Northern Chilean Andes

Intensely arid climates in western South America extend from 15°S in southern Peru to around 29°S in Chile. True absolute desert (without vegetation except along main water courses as the Río Lluta, Río Azapa, and Río
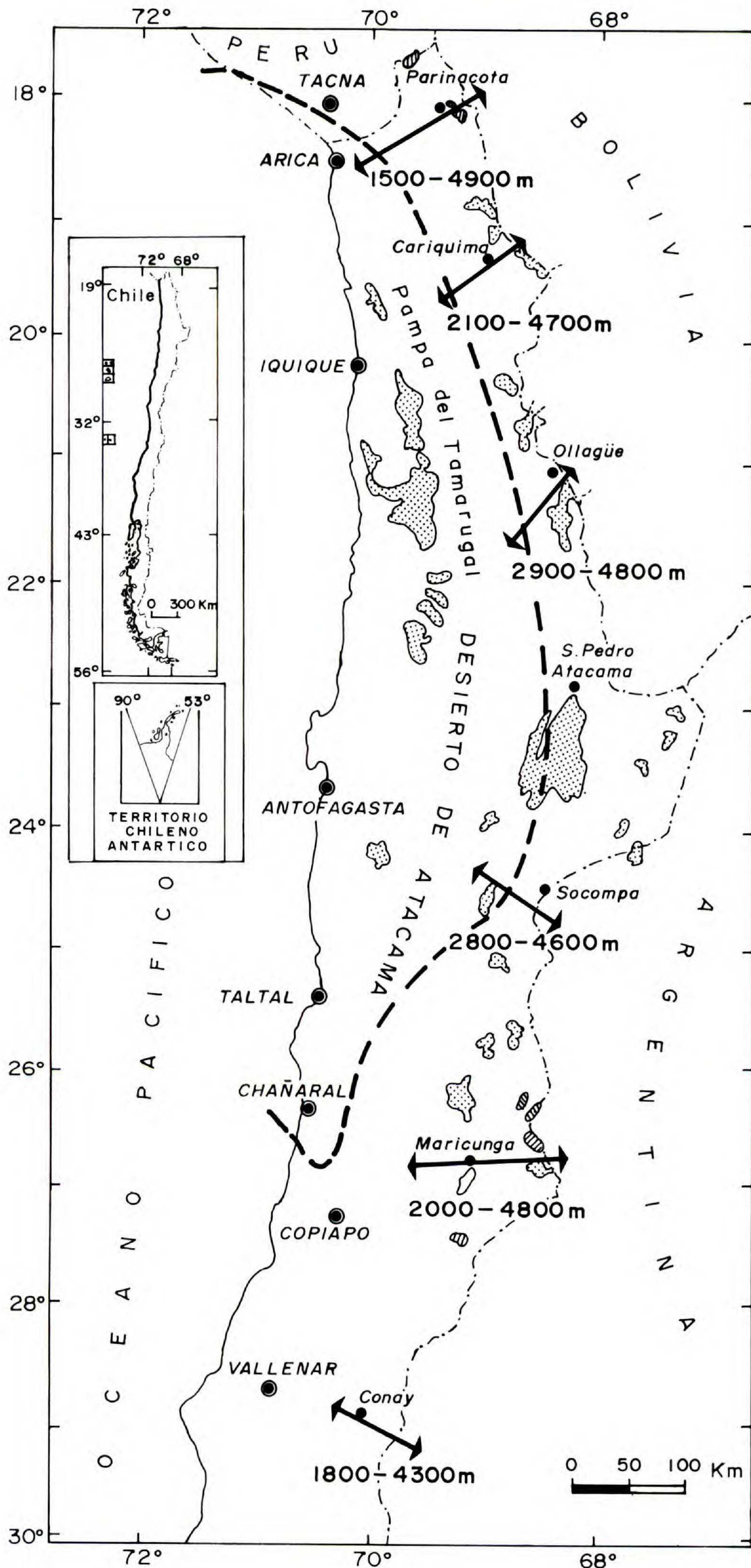
Loa, or in coastal fog pockets such as Paposo and Taltal) occurs south of 17°S to 25°S (Fig. 1). The desert rises abruptly from a narrow coastal strip to 1,500 m at the Arica deflection (18°S) in northern Chile and reaches a maximum elevation of 3,000 m at 24°–25°S, in from the coastal cities of Antofagasta and Taltal. South of 25°S aridity decreases again.

The Chilean–Peruvian arid diagonal is a "rain shadow" and a "cold air" desert (Rauh, 1983). The present climate (Figs. 2, 3) is determined primarily by the annual behavior of the Intertropical Convergence situated over equatorial latitudes (Gomez & Little, 1981) which brings moisture from the northeast, and by a Polar front bringing precipitation from the southwest, together with the interplay of these precipitation sources and the major ocean currents. South of 24°–25°S, most precipitation is received during the winter months (May–August; "invierno chileno") from a northward extension of the Polar front. Consequently, the climate is essentially an arid version of the true Mediterranean climate further south at 30°–38°S. Here there is no east–west reduction in rainfall (Fig. 2). Most precipitation above 3,000 m in the Chilean Andes for these latitudes is in the form of snow.

North of 24°S, where a southward extension of the Intertropical Convergence during the summer months comes into play and the Polar front is negligible, precipitation is received during the summer months (November–March; "invierno boliviano") as rainfall below 4,000 m or as transient snow and hail above 4,000 m. The winters are cold and dry. At these latitudes the Andes generate a rain shadow by forcing moisture-laden air from the northeast to rise and cool on their eastern slopes. The greatly diminished saturated air masses ascending onto the western side of the

Andes undergo adiabatic heating, further reducing potential precipitation. As the air masses reach lower elevations towards the Pacific, they are further dried by cold surface waters from the Circumantarctic Current carried northward by the equatorward-running Humboldt Current (Peru Current) (Zinsmeister, 1978) and by cold bottom water upwelled from the Pacific by the Humboldt Current as it is deflected away from the coast by the Coriolis effect in subequatorial latitudes. As a result of these features and southward weakening of the Intertropical Convergence, the Chilean Andes north of 24°–25°S are characterized by steep east–west and north–south reductions in precipitation (Fig. 2). Typical of the east–west gradient, recorded annual precipitation for Parinacota (18°S), situated at 4,395 m, is 372 mm. Murmuntane, situated at 3,280 m and less than 100 km to the west, receives only an average of 156 mm of rainfall annually, while mean annual rainfall for Arica on the coast (29 m) is less than 1 mm. Southwards at 21°S, recorded annual precipitation for Cebollar at 3,730 m is 53 mm, while at 24°S (at Imilac, 3,232 m) recorded annual rainfall is 2.4 mm.

In the northern Chilean Andes, as a result of reduced cloudiness due to higher than average adiabatic heating, the normal latitudinal decrease in temperature is essentially absent to at least around 24°S (Fig. 3) (from 25° to 28°S there are too few temperature records for the Andean highlands). This fortuitous situation avails easy temperature control of comparisons of diversity with increasing aridity. The average lapse rate above 1,000 m is about 6.5°C per 1,000 m increase in elevation. Below 1,000 m, where coastal fog results in abnormal cooling, the lapse rate is lower. Mean annual temperature at Murmuntane (3,280 m) is 9.7°C. Mean annual temperature at Parinacota (4,395 m) is 2.5°C.

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FIGURE 1. *Location and altitudinal ranges of transects in the northern Chilean Andes. Heavy dashed line denotes upper limit of absolute desert in the Andean highlands. Stippled areas: major present-day salt lakes. Hatched areas: freshwater lakes.*
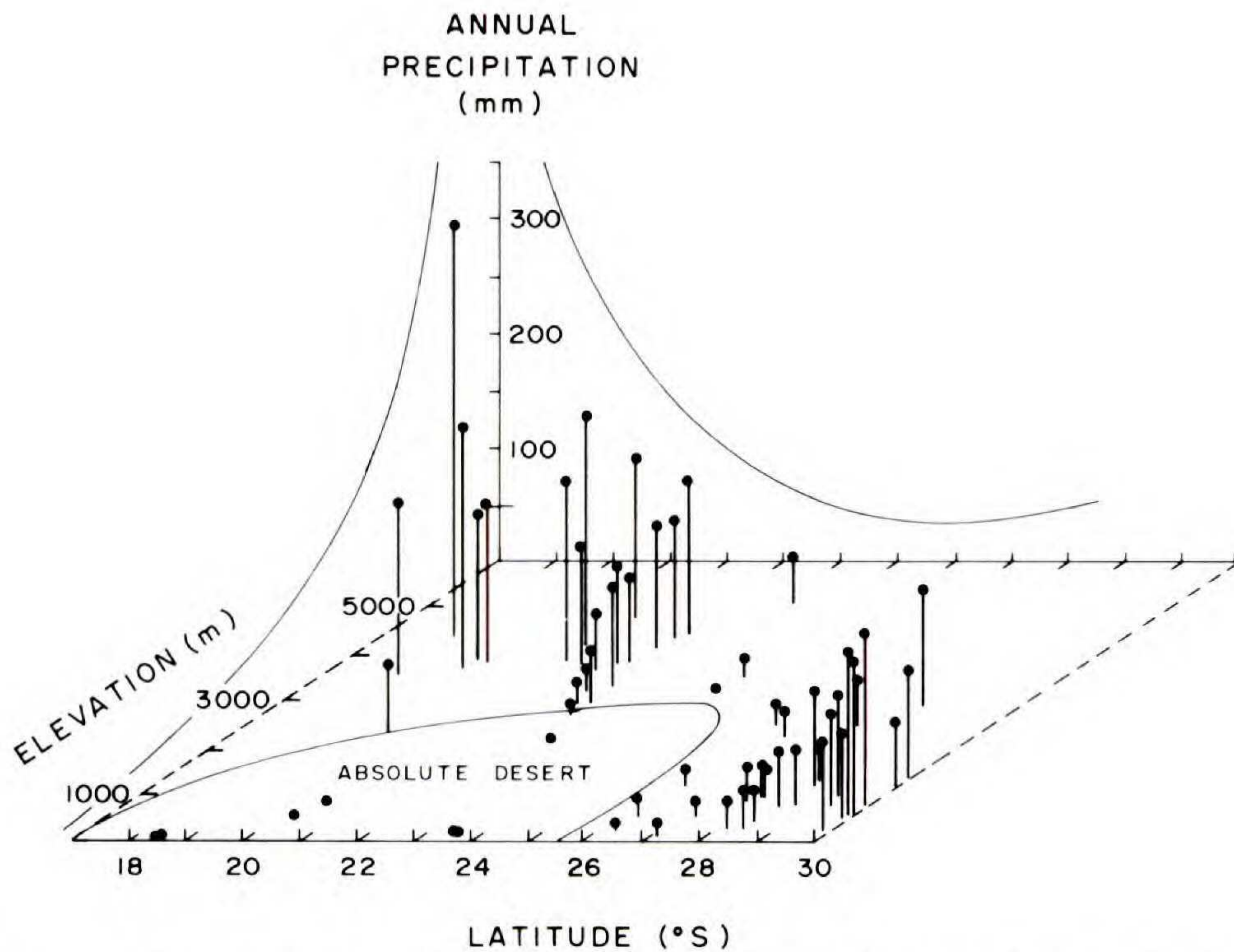
FIGURE 2.   Mean annual precipitation related to elevation and latitude in northern Chile. Data from Ministerio de Obras Publicas (MOP), Santiago, and di Castri & Hajek (1976). Precipitation data unavailable for the Andean highlands between 26° and 28°S.

II: HISTORICAL DEVELOPMENT OF ARIDITY IN THE NORTHERN CHILEAN ANDES

Proposed timetables for development of arid climate in western South America span Miocene (e.g., Muizon & DeVries, 1985) to Quaternary initiation dates (e.g., Ochsenius, 1983a). Ochsenius & Santana (1974), Ochsenius (1983b), and Axelrod (1979b) agree that maximum aridity was reached very recently.

EMERGENCE OF THE ANDES

That many of the high Andean summits rose rapidly and only very recently is critical to understanding the development of harsh arid climates at subtropical latitudes in western South America.

From the late Cretaceous into early Paleocene times, volcanic rocks and associated sediments, deposited close to the present continental margin in Mesozoic times as a result of the closure of the Nazca and American plates (Rutland, 1971; Mortimer et al., 1974), were uplifted to form a proto-Andean divide west of the present Cordillera Occidental

(Mortimer, 1980). This primitive axis, however, was almost entirely eroded away, leaving the Altos de Camilica Formation in southern Peru (Tosdal et al., 1984) and the Putani Formation east of Arica (Mortimer & Saric, 1972). The modern landscape differentiated
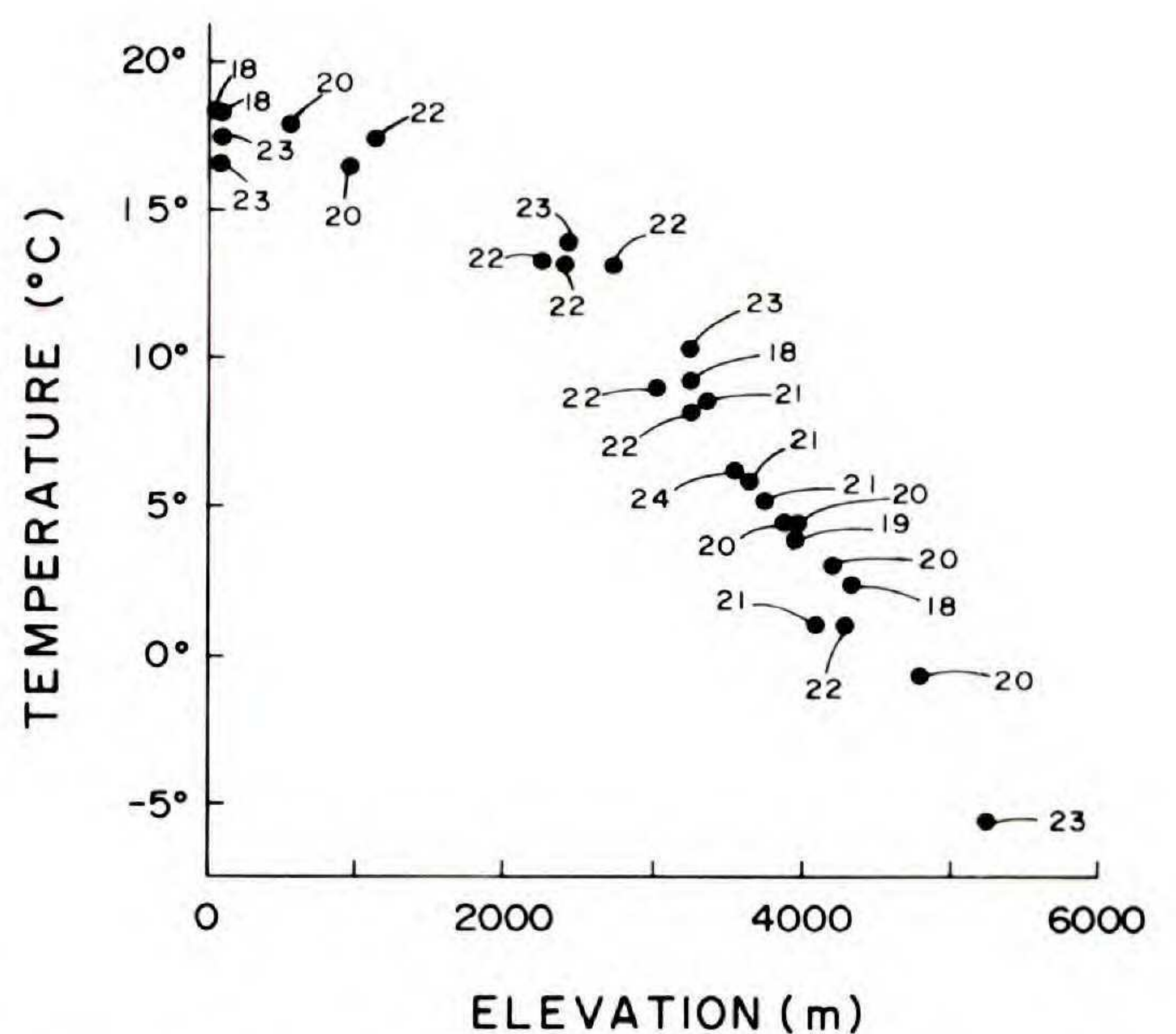

FIGURE 3.   Mean temperature plotted against elevation for areas between latitude 18° and 24°S in the northern Chilean Andes. Data sources as for Figure 2. Data point for 5,300 m at 23°S is from Corrida de Cori (Ruthsatz, 1977), Argentina, close to the Chilean border. The numbers associated with each datum point indicate the corresponding latitude.

initially in the late Paleocene–early Miocene interval. It comprises (a) the nonvolcanic Cordillera de la Costa, (b) a low-lying depositional basin referred to as the Pampa de Tamarugal in northern Chile or Llanuras Costaneras in southern Peru, (c) the precordillera, a loosely defined transition zone at 2,000–4,000 m, and (d) the parallel cordilleras Occidental and Oriental with summits close to 7,000 m. These cordilleras are separated by (e) a broad intervening high-altitude plain, the Altiplano, of some 500,000 km² (Allmendinger, 1986) at 3,700–4,000 m (Fig. 4).

The Cordillera Occidental and the Cordillera Oriental emerged relatively late after two major focal points of rhyolitic volcanic activity developed in the late Oligocene and into the early Miocene (Tosdal et al., 1984; Naranjo & Paskoff, 1985) following extensive north–south block faulting and differential uplifting (Mortimer & Saric, 1972). Such activity persisted well into the late Miocene and early Pliocene (Megard et al., 1985), by which time deposition of sediments derived from the surrounding eroding volcanic axes produced the Altiplano (Fig. 4). During the same epoch, lava flows moving westward and sediments from the Cordillera Occidental backed up against the Cordillera de la Costa (Naranjo & Paskoff, 1985), elevating the northern part of the Pampa de Tamarugal in Chile and the Llanuras Costaneras in southern Peru.

The major increase in height in the Andes, nevertheless, occurred only as of the middle Miocene and onward (Mortimer et al., 1974) in north Chile and the Pliocene in southern Peru (Tosdal et al., 1984) as the result of andesitic volcanism (Fig. 4). Andesitic activity continued across the Cordillera Occidental and Cordillera Oriental throughout the Pliocene and Pleistocene into the Holocene, giving rise to the some 800 volcanoes present in northern Chile. Over 30 of these exceed 6,000 m elevation. Tosdal et al. (1984) estimated that the southern Peruvian Andes were uplifted 0.06–0.19 mm per year throughout the Neogene. The Cordillera Occidental at its southern edge is thought to have increased in height by 0.5 mm per year as of Holocene times (Rutland et al., 1965).

MIOCENE CLIMATES

Although significant uplifting had occurred by the Miocene, there is no evidence at this stage of the strong east Andean rain shadow seen in the Andes today. Axelrod (1979b) reviewed the limited paleobotanical evidence for the Miocene. Berry (1919) described leaf remains from the Tumbez area in northern Peru. Included is material identified as *Annona*, *Banisteriopsis*, *Ficus*, *Persea*, and *Styrax*. Although Berry's identifications require verification, the leaf types present are indicative of a fairly closed tropical viney forest and of productive environments.

A second flora studied by Berry (1917, 1939) from Potosí, Bolivia, now above 4,000 m and immediately to the east of the Cordillera Occidental, was considered by Ahlfeld (1956) to be of Miocene age and would have thus been deposited during the early phases of the uplifting of the Altiplano. It reportedly contains *Calliandra*, *Cassia*, *Copaifera*, *Dalbergia*, *Escallonia*, *Passiflora*, *Terminalia*, *Inga*, and *Weinmannia*. Today similar floras strongly dominated by woody leguminous taxa typically occur in neotropical formations under high rainfall regimes but usually with a distinct dry season in the Venezuelan llanos and adjacent Orinocan forests and areas transitional between Amazonia and the Brazilian Planalto. Elements reminiscent of *Weinmannia*, *Escallonia*, and *Inga* suggest that a semiseasonal forest gave way to a middle-altitude montane forest similar to that seen today further north in the Andes in Colombia where rainfall is very high.

A third flora, from Psillypampa, Bolivia, still further to the east of the main Andean axis, today at 2,600 m, was regarded as Pliocene age by Berry (1922) but suspected by Axelrod (1979a) as possibly of Miocene age. It contains material identified as *Heliconia*, *Myrica*, *Pisonia*, and *Pithecellobium* and many other genera with fairly small leaves. For the Miocene then, there appears to have been a transition from viney forest on the extreme Pacific border, into semiseasonal vegetation types at mid elevations on the Altiplano, and finally into more xeric, small-
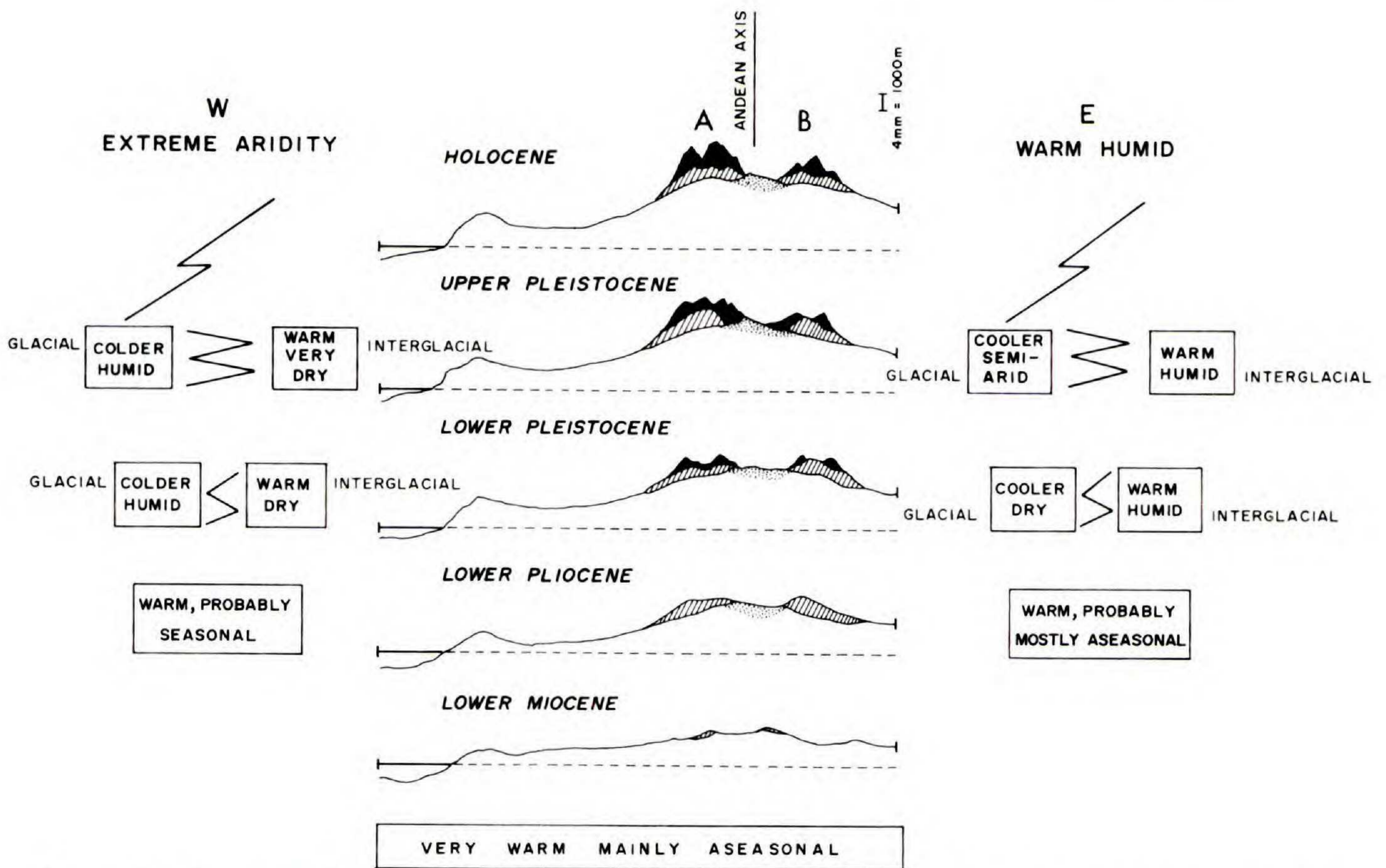
FIGURE 4. Stages in the evolution of the Cordillera Occidental (A) and Cordillera Oriental (B) as of the Miocene and climatic tendencies west and east of the northern Andes during the Quaternary. Hatched areas: rhyolitic volcanic activity. Stippled areas: Atiplano. Black areas: andesitic volcanoes.

leaved forms at lower elevations on the eastern side of the Altiplano. This suggests that, in contrast to today, the western side of the Miocene Andes may have been wetter than the eastern side.

The expected positions and water temperatures of currents in the Pacific Ocean support the above interpretation. Prior to the consolidation of the Antarctic Icesheet, the west wind drift is believed to have lain further south than today; moreover, as Zinsmeister (1978) suggested, cold surface waters would have been directed between East and West Antarctica rather than up the South American coast. With a less active and considerably warmer Humboldt Current in the Miocene, the counter-running warm current bathing the coasts of Ecuador and Peru today most likely extended south of its present position, very possibly engendering precipitation patterns similar to that in recent El Niño events (Cane, 1983), which brought torrential rains to coastal and lowland areas of southern Ecuador and northern Peru (Rasmusson & Wallace, 1983).

A warm, wet Miocene for the western flanks of the subtropical Andes finds good support from marine fossils deposited in high coastal cliffs in northern and central Chile during marine transgressions (Mortimer, 1972) and in the related Pisco Formation in the Llanuras Costaneras of southern Peru (Muizon & DeVries, 1985). At 30°S on the coast of Chile, dendrophyllid corals accompanied a warm-water ostracod fauna, of which some subtropical elements extended as far south as 47°S (Herm & Paskoff, 1967; Herm, 1969). The Pisco Formation contains turtles, sloths, terrestrial carnivores, and other large-bodied animals that could only have existed under fairly productive environments. Vertical incisions up to 1,000 m deep traverse the central depression in northern Chile (e.g., quebradas Vitor, Azapa, Lluta, Camarones). These, which geologists agree are indicative of high pluviosity, were initially cut down in the Miocene (see Mortimer, 1973; Paskoff & Naranjo, 1979; Naranjo & Paskoff, 1980a). Finally, the Miocene was the time of maximum copper enrichment in the Chilean Andes

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(Clark et al., 1967). The high water table that this process requires and an active period of erosion seen in canyon development seem to be indisputable evidence against dry climates in the western deserts at this stage.

PLIOCENE CLIMATES

The Pliocene is poorly known for arid subtropical latitudes in western South America. Marine faunas on the Chilean coast at 30°S (Herm, 1969) and in the Pisco Formation in southern Peru (Muizon & DeVries, 1985) show declines in species richness and an influx of elements from cooler waters at the Miocene–Pliocene boundary. Zinsmeister (1978) related such changes to increased incorporation of cold water into the Humboldt Current due to northward displacement of the west wind drift and reduced flow through Drake Passage. Certain periods in the Pliocene in the Colombian Andes, situated away from the influence of the Humboldt Current, saw lower tree lines than at present and the first appearance of a high-elevation flora (Hooghiemstra, 1984). Thus changes in marine faunas along the Pacific coast must have been due at least partially to a general global trend toward climatic cooling. Climates were evidently drier than in the Miocene—canyon cutting in the Atacama ceased abruptly at this stage (Mortimer, 1973). *Vallea, Borreria, Niphogeton,* and *Eryngium,* genera considered indicative of open conditions, became abundant occasionally in high-elevation Colombian forests (Hooghiemstra, 1984). During this period large mammals (*Equus, Megatherium*) appeared in the present area of the Atacama desert. This scant information for the Pliocene suggests a gradual transition from the closed Miocene forests into more open, savannalike vegetation at low elevations, with small, evergreen treelets developing at mid elevations. The presently disjunct montane genus *Kageneckia* (Rosaceae), which occurs in central Chile and again in eastern Bolivia and southern Peru, could have been present in these Pliocene montane forests. *Prosopis,* the only surviving tree genus at low elevations in the Atacama today, probably dates to lowland Pliocene vegetation.

PLEISTOCENE–HOLOCENE CLIMATES

The fairly uneventful, drier and cooler, but far from hyperarid Pliocene of the western margin of subtropical South America gave way to a Pleistocene characterized by marked alternating wet and dry periods.

For tropical and subtropical lowland areas east of the Andes in South America the glacials were *cold-dry* times of forest contraction, while the interglacials were *wet-warm* times of forest expansion (Damuth & Fairbridge, 1970; Colinvaux, 1979; Ab'Saber, 1982; Prance, 1982). It has not been sufficiently appreciated that the wind systems proposed by Damuth & Fairbridge (1970) to account for dry glacial periods in the Amazon Basin predict precisely the opposite climatic trends for corresponding periods on the western side of the Andes, i.e., *warm-dry* periods alternating with *wet-cold* periods (Fig. 5).

During the glacials, the Damuth & Fairbridge model sees a low-pressure focus over Antarctica moving northward, bringing increased moisture from a southwestern source to mid- and subtropical latitudes in South America (Fig. 5). Because the cordilleras were now strongly elevated, the destination of much of this precipitation would have been the western side of the central Andes. Geological evidence suggests that the Atacaman area indeed experienced very wet climates in the Pleistocene. Many of the salt lakes (salares) presently occupying 2,800 km² bear extensive deposits of Pleistocene lacustrine and diatomaceous earth (Stoertz & Ericksen, 1974; Naranjo & Paskoff, 1980b). Analyses of old shoreline lines (Tricart, 1969) indicate that approximately one-half of the present salares in northern Chile (e.g., salares de San Martín, Ollague, Uyuni, Coipasa) formerly constituted extensive, deep, perennial lake systems (Stoertz & Ericksen, 1974). Wet glacial periods on the western side of the central Andes are also suggested by the fact that the Pleistocene snow line was depressed to a greater
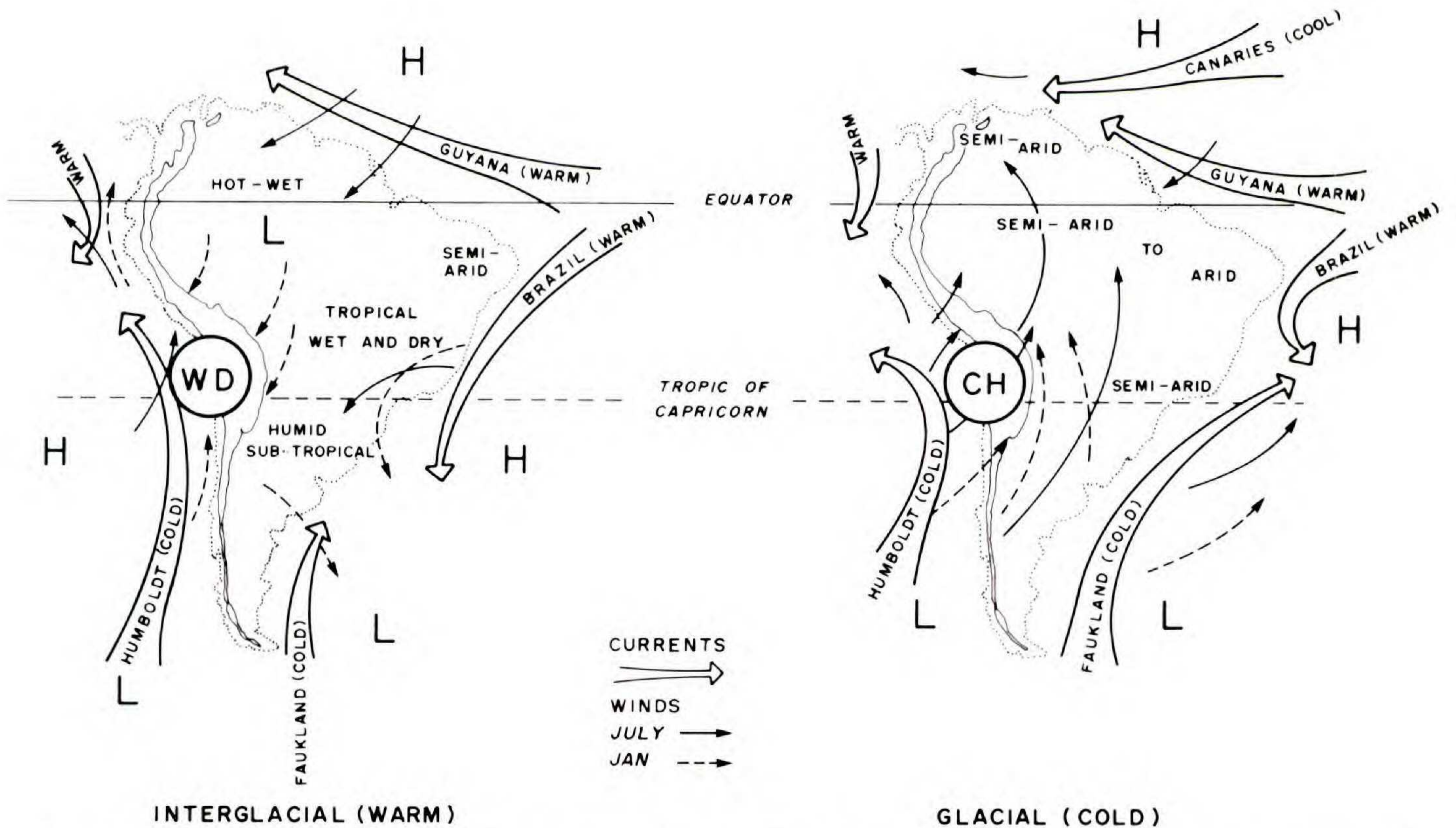
FIGURE 5. *Probable glacial and interglacial climates for the present Atacama desert region (area under large circles) in relation to the rest of South America. WD: warm-dry. CH: cold-humid. Modified from Damuth & Fairbridge (1970).*

extent on the western side of the Andes (Hastenrath, 1967).

The pollen record for the Andes, although still sparse, is also consistent with strong east–west climatic differentiation in the northern Andes during the Pleistocene. Heusser (1983) provided evidence of northward migrations of *Nothofagus* and *Podocarpus* in central Chile during glacial phases. This evidence indicates wet-cold climates for the western side of the Andes. On the eastern side of the subtropical Andes, in contrast, drought-tolerant taxa appeared on the border of the puna in the Junín area in Peru (Hansen et al., 1984) and close to the Bolivian–Peruvian border (Graf, 1981) during cold periods of the Pleistocene and of the Holocene, respectively. Late glacial assemblages from eastern Patagonia at 41°S are also consistent with colder and drier conditions than today (Markgraf, 1983). Eastern high elevations at Mediterranean latitudes, however, and the extreme edge of the puna in Jujuy (unlike the puna further north in Bolivia and Peru, and the Patagonia further south) were wetter than today during cold periods (Markgraf, in press). Such simulta-

neously wetter climates on the western (cf. Heusser, 1983) *and* eastern sides of the Andes at Mediterranean latitudes (out of the range of the Intertropical Convergence and hence very dry during the interglacials) are not unexpected; the greatly increased westerlies there relative to interglacial periods would have increased precipitation on the Pacific side of the Andes and augmented that making its way across the Andes.

As each interglacial ensued and climates warmed, the southwesterlies would have resumed their present position (Fig. 5) with the Intertropical Convergence coming back into play in the northern Andes as seen today. Because the Andes rose significantly during the several wet-cold and warm-dry cycles of the Pleistocene, east–west climatic differentiation must have increased as the Pleistocene progressed. As a result, aridity should have intensified at each new interglacial.

Throughout the climatically turbulent Pleistocene, nevertheless, the Atacaman region continued to support large mammals, including *Mastodon* and *Macrauchenia* (Mares, 1985). That such animals did not

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TABLE 1. *Comparison of the number of species present (species richness) for the total vascular flora and for zonal and azonal (bog) components of each flora considered separately at different latitudes in the northern Chilean Andes. Number of species per genus and number of genera per family are also given for the total flora at each latitude.[1] See Figure 1 for exact locations. Latitude 18°S receives the most precipitation; latitude 24°S receives the least precipitation.*

	Summer Precipitation				Winter Precipitation	
	18°S	19°S	21°S	24°S	26°S	28°S
Total flora						
Number of species	391	219	164	77	144	270
Number of genera	195	138	110	55	90	162
Species/genus	2	1.6	1.5	1.4	1.6	1.7
Number of families	64	53	37	30	42	58
Genera/family	3	26	3	1.8	2.1	2.8
Zonal flora						
Number of species	333	190	141	59	110	200
% of total flora	85.2	86.7	86	76.6	76.4	74.1
Azonal flora (bogs)						
Number of species	58	29	23	18	34	70
% of total flora	14.8	13.2	14	23.4	23.6	25.9

[1] Species/genus and genus/family ratios exclude some Cactaceae of doubtful generic affinity.

become extinct until the end of the Pleistocene (Ochsenius, 1983a) agrees entirely with Axelrod's (1979b) suggestion that the climate on the western slopes of the northern Chilean Andes reached its present intensely arid state only very recently in Holocene times.

III: PATTERN OF DIVERSITY IN THE NORTHERN CHILEAN ANDES

SPECIES RICHNESS

Excluding a small number of systematic problems that still require attention, the succession of vegetation belts (desert scrub, Andean, high Andean) up from the desert edge to the upper vegetation limit on the six transects (Fig. 1) yielded 769 species in 290 genera of vascular plants. Five hundred twenty-one species have been collected on the four northernmost summer-rainfall gradients (Table 1). Here species richness peaks at mid elevation, where conditions are intermediately arid and cold (Fig. 6). The resultant curves tend to be steeper towards the north where the east–west precipitation gradient is most severe.

Three hundred twenty-seven species occur on the winter-rainfall transects at 26°S and

28°S; here maximum species richness, in contrast with the northern transects, occurs at lower elevations. These winter-rainfall transects nevertheless tend to show a mid-elevation bulge of their own which reflects the lowermost elevation of permanent winter snow in these areas.

Latitudinally, species richness drops off by 80% from 18°S (maximum rainfall from the
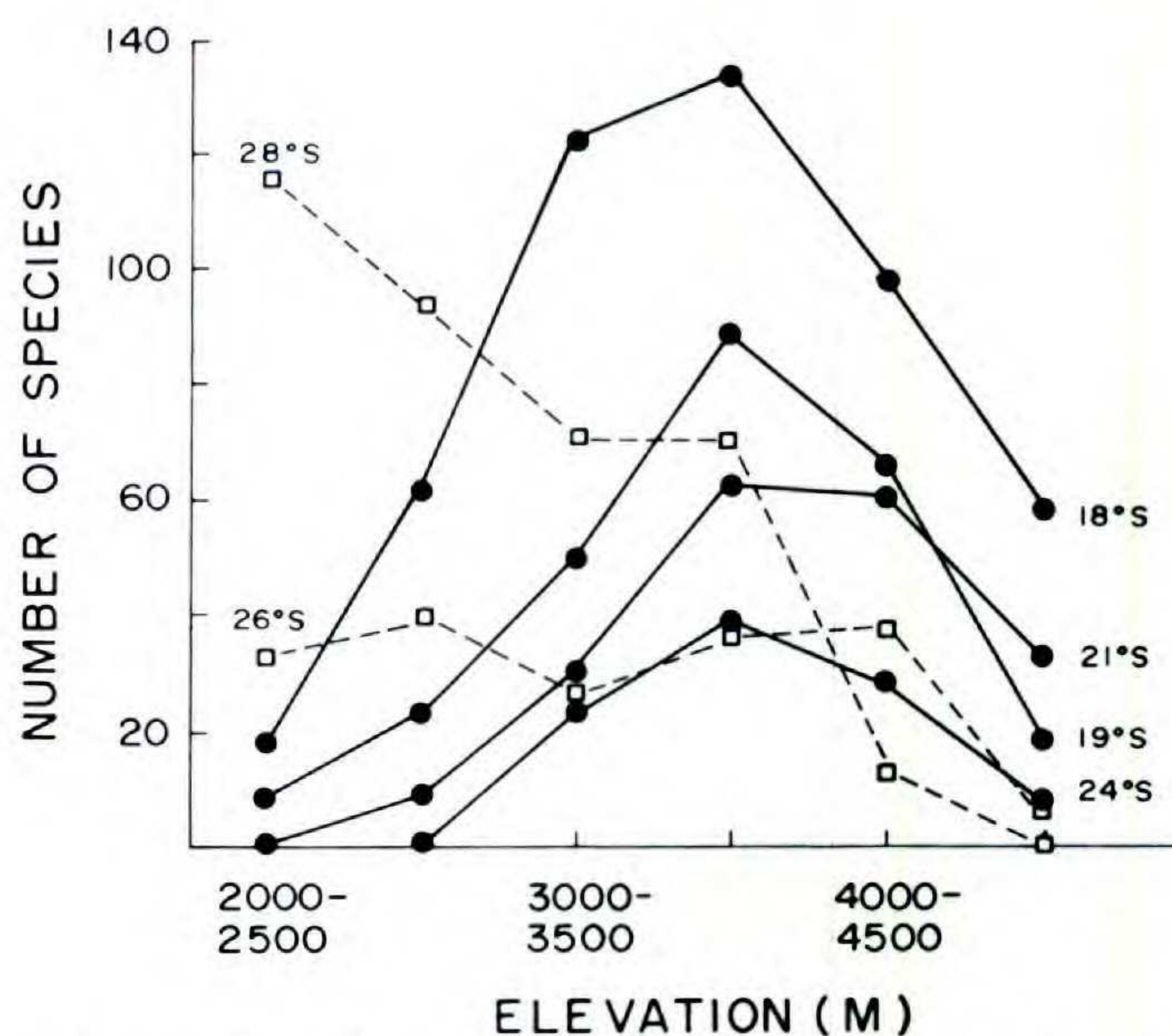

FIGURE 6. *Variation in number of species (species richness) with elevation at different latitudes in the northern Chilean Andes.* ● = *summer-rainfall zone (solid line);* □ = *winter-rainfall zone (broken line).*

TABLE 2. Life forms on the western (Chilean) and eastern (Argentine) side of the northern Andes. Data for the Chilean region correspond to the floras present on the six transects in Figure 1. Data for the Argentine region are from Ruthsatz (1977). The G-tests compare the percentage of a given life form for the pair of floras indicated. Estimates of precipitation for the western floras are averages of amounts used in the regressions in Table 3.[1] Estimates for the eastern floras are averages of weather station data reported in Ruthsatz (1977).

	Western Andes			Eastern Andes	G-test (Western Comparisons)			G-test (East–West Comparisons)	
	18–19S (A)	21–24S (B)	26–28S (C)	22–24S (D)	A vs. B	A vs. C	B vs. C	D vs. A	D vs. B
2,000–3,000 m									
Estimated precipitation	68 mm	6 mm	—	200 mm					
Shrubs & trees	28 40.6%	7 70.0%	62 42.5%	53 40.8%	NA[2]	0.08; NS[3]	NA	NA	NA
Perennial herbs	24 34.8%	2 20.0%	41 28.1%	58 44.6%	NA	1.00; NS	NA	NA	NA
Annual herbs	17 24.6%	1 10.0%	43 29.4%	19 14.6%	NA	0.50; NS	NA	No Significant Differences	NA
	(69 spp.)	(10 spp.)	(146 spp.)	(130 spp.)					
3,000–4,000 m									
Estimated precipitation	153 mm	30 mm	—	249 mm					
Shrubs & trees	70 32.4%	32 36.0%	54 35.8%	84 34.1%	0.30; NS	0.48; NS	0.00; NS		0.06; NS
Perennial herbs	107 49.5%	32 36.0%	61 40.4%	131 53.3%	4.73*	3.00; NS	0.22; NS		5.92*
Annual herbs	39 18.1%	25 28.1%	36 23.8%	31 12.6%	3.67; NS	1.84; NS	0.52; NS		10.21***
	(216 spp.)	(89 spp.)	(151 spp.)	(246 spp.)					
4,000–5,000 m									
Estimated precipitation	266 mm	97 mm	—	330 mm					
Shrubs & trees	25 17.4%	32 37.6%	25 26.0%	42 17.9%	11.48***	2.6; NS	2.83; NS		12.68***
Perennial herbs	107 74.3%	43 50.6%	48 50.0%	175 74.8%	13.11***	14.80***	0.02; NS		16.16***
Annual herbs	12 8.3%	10 11.8%	23 24.0%	17 7.3%	1.84; NS	11.80***	4.60*		1.52; NS
	(144 spp.)	(85 spp.)	(96 spp.)	(234 spp.)					

[1] Precipitation data unavailable for 26–28S; hydrological considerations (Ministerio de Obras Publicas, Santiago) suggest that this area is intermediate between 18 and 19S for precipitation.
[2] G-test not applicable.
[3] Significance levels for G-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.

Intertropical Convergence) to 24°S (minimum rainfall from the Intertropical Convergence) (Table 1); however, recuperation is rapid around 26°S and 28°S in the influence of the winter-rainfall pattern. Species/genus ratios are low in all cases (1.4–2; Table 1), although *Senecio* (18°S: 26 species), *Adesmia* (28°S: 13 species), *Nototriche* and *Werneria* (18°S: 12 species each), *Stipa* (18°S: 11 species), *Deyeuxia* and *Baccharis* (18°S: 7 species each), *Calandrinia*, *Festuca*, and *Solanum* (18°S; 7 species each), and *Chaetanthera* (28°S: 7 species) are speciose. Under both precipitation regimes, as aridity increases, trends for fewer species per genus and fewer genera per family are seen (Table 1). Thus fewer genera and fewer species have survived in the most arid regions, and/or these appear to have undergone less local speciation. Precise records of precipitation for the highlands at 28°S are unavailable. Hydrological estimates (Ministerio de Obras Publicas, Santiago) suggest levels roughly similar to those midway between 18° and 19°S. Species richness is lower at 28°S than midway between 18° and 19°S, indicating that the decline in species richness from 18° to 24°S is probably slightly inflated by a small latitudinal effect independent of precipitation.

By comparing floras on the east side and west side of the Andes for areas with equivalent precipitation, the degree to which historical and biogeographical factors contribute to present richness patterns may be assessed. Similar amounts of precipitation are received at 18°–19°S on the Chilean side of the Andes and at 21°–24°S on the Argentinian side at 4,000–5,000 m (Table 2). Nevertheless, around a third more species occur on the eastern side, which experienced less severe fluctuations during the Pleistocene. Such lower richness levels on the western side of the Andes undoubtedly also reflect reduced north–south migration possibilities there on account of the desert extending above 3,000 m at 24°S (Arroyo et al., 1982; Villagrán et al., 1983). Thus, in addition to the direct effect of lowered precipitation on species richness, there seems to be a substantial indirect effect of the evolution of aridity.

TABLE 3. *Best fit regressions of number of species (species richness) on mean annual precipitation in the northern Chilean Andes. Each regression is based on species numbers at 18°S, 19°S, 21°S, and 24°S. Mean annual temperature for these latitudes is relatively constant with elevation (see Fig. 3). y = number of species; x = mm precipitation. Degrees of freedom for all regressions = 2.*

Elevation	Regression	F-ratio[1]
2,000–2,500 m	$y = -0.17e^{0.05x}$	23.95***
2,500–3,000 m	$y = -0.60x^{0.98}$	3.78 NS
3,000–3,500 m	$y = 3.09e^{0.01x}$	4.61*
3,500–4,000 m	$y = 0.42x + 32.67$	18.09***
4,000–4,500 m	$y = 2.29x^{0.38}$	11.27**
4,500–5,000 m	$y = 0.12x + 5.03$	6.03*

[1] Significance levels for regressions: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.

A more precise appreciation of the combined indirect and direct effects of aridity on species richness in the northern Chilean Andes may be obtained by relating species richness to precipitation for areas with similar mean annual temperatures. Most regressions (best fits varied from a linear, through semilog to log–log model) (Table 3) were significant. The degree of curvature where fits were curvilinear, however, was always very shallow. The overall regression of species richness on precipitation, combining all elevations, was also highly significant ($F = 14.087$; d.f. = 22; $P = 0.002$), emphasizing very high penetrance of precipitation on species richness on a biogeographical scale. Aridity, moreover, completely obliterates the effects of temperature regionally. In the multiple regression of species richness on mean annual precipitation and mean annual temperature as independent variables ($y = 0.216x_1 + 0.017x_2$; d.f. = 21; $P = 0.005$, where x_1 is mean annual precipitation and x_2 is mean annual temperature), the partial regression coefficient for precipitation was highly significant ($P = 0.007$), whereas that for temperature (normally a strong determinant of species-richness patterns along elevational gradients) was nonsignificant ($P = 0.991$).

There are also clear reductions in total plant cover with aridity (Fig. 7). In the most benign of the wettest areas in the northern Andes, total cover does not exceed 50%.
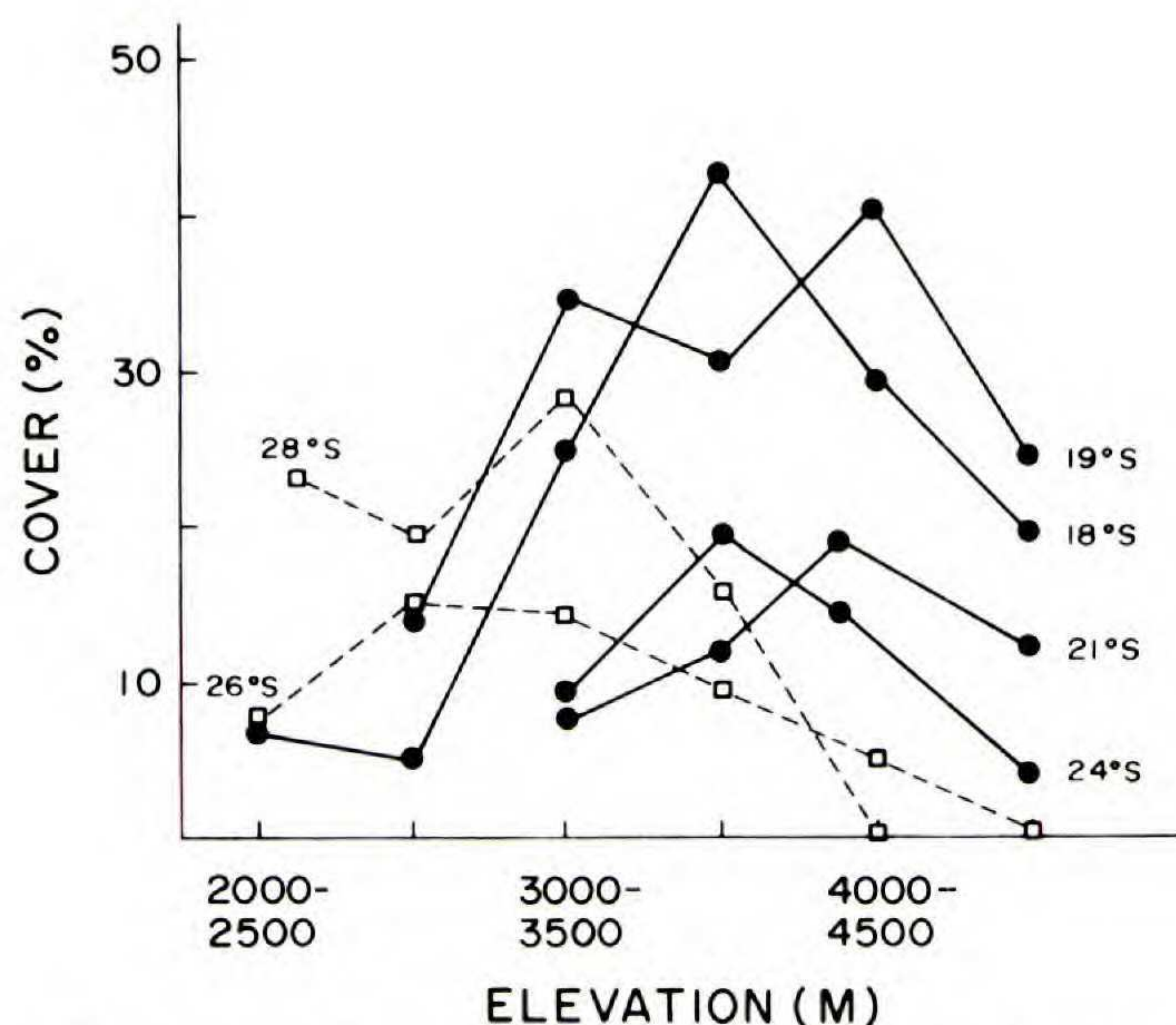
FIGURE 7. *Variation in plant cover (% of ground vegetated) with elevation at different latitudes in the northern Chilean Andes.* ● = *summer-rainfall zone (solid line)*; □ = *winter-rainfall zone (broken line).*

However, at 24°S, less than 25% of total surface is covered. The regression of plant cover on plant species richness ($y = 0.22x + 8.21$; $F = 12.31$; d.f. = 17; $P = 0.003$) was highly significant. However, as indicated by the regression coefficient (also compare Figs. 6, 7), reduction in plant cover and species richness reduction are not strictly parallel. This suggests that although relatively few species survive on the most arid sectors of the northern Andes, some (e.g., *Adesmia polyphylla, Stipa frigida, Philippiamra fastigiata*) thrive. Species that are rare at latitudes 18°S and 19°S (e.g., *Portulaca philippii, Solanum phyllanthum, Dunalia spinosa*, many species of *Senecio*), on the other hand, are conspicuously absent on the drier 21°S and 24°S transects. Stochastic effects bearing on the smaller populations of such species perhaps have prevented survival in the most arid habitats. This last factor probably contributes to the lower species/genus ratios seen with severe aridity.

HIGH ANDEAN BOGS VERSUS
ZONAL VEGETATION

In the wettest area of the northern Chilean Andes (18°S) above 4,000 m, previous freshwater lakes dating to the pluvial cycles of the Pleistocene support azonal cushion bogs (bo-

fedales). In the driest areas (24°–26°S) such lakes have been reduced to salares with small marginal patches of bog vegetation. These important grazing resources for the Altiplano economy (Castro et al., 1982) contain such typical species as *Gentiana sedifolia, Azorella trifoliolata, Lachemilla* spp., *Werneria* spp., and *Colobanthus quitensis*. They are unique to the central and drier sectors of the southern Andes and are unknown in the far northern Andes, where azonal and zonal vegetation types tend to intergrade imperceptibly (Cleef, 1980).

Despite reduction in area suitable for development of bog vegetation towards 24°S in the northern Andes and the greater dependence of bog elements on fresh water, bog habitats have lost proportionately fewer species than zonal habitats (Table 1). For example, bog species constitute only 14.83% of the total flora at 18°S in comparison with 23.38% at 24°S.

Relatively lighter losses in species richness in the bog floras possibly result from new introductions repeatedly offsetting losses due to reduced habitat size. Figure 8 plots floristic divergence for zonal and azonal (bog) elements for all possible pairs of the six transects against the geographical distance separating each pair of transects. For both vegetation types, floristic divergence increases with distance; however, the bog floras are notably less disparate than the zonal floras for equivalent separation distances. Floristic affinity of the bog floras is higher because of lack of local endemic speciation and because the latitudinal ranges of bog species along the Andes are wider in comparison with zonal elements (Arroyo et al., 1982). The broader latitudinal ranges of bog species, in turn, may be related to aspects of reproductive biology. Many bog elements are strongly autogamous (e.g., *Colobanthus quitensis, Gentiana prostrata, Cardamine glacialis*), greater reliance on wind-pollination is also evident (Arroyo et al., 1983), and some dominant bog species (e.g., *Distichia muscoides, Oxychloe andina*) are clearly adapted for bird dispersal. These three features should facilitate long-distance dis-

persal between the islandlike high-Andean bogs, thereby maintaining their floras relatively homogeneous. They should also promote reintroductions of species lost due to reduced habitat size.

LIFE FORMS—INTERANDEAN TRENDS

Table 2 compares life-form spectra for the wettest (18°–19°S) and driest (21°–24°S) extremes of the summer-rainfall area (comparison A vs. B) and for the summer-rainfall areas vs. the winter-rainfall area (26°–28°S) (comparisons A vs. C & B vs. C) at three elevational levels. Comparing the wet and arid extremes of the summer-rainfall area, perennial herbs are statistically underrepresented at the arid extreme for 3,000–4,000 m and 4,000–5,000 m. Because of small numbers of species, the data for 2,000–3,000 m could not be tested statistically; however, a similar trend is evident with relatively fewer perennial herbs occurring at 21°–24°S. The difference is most pronounced in the upper Andean belt (4,000–5,000 m) and along the desert edge (2,000–3,000 m).

Woody species, in contrast, tend to be more strongly represented as aridity increases; the trend is clear in the driest (2,000–3,000 m) of the three vegetation belts and where aridity is overlain with cold stress (4,000–5,000 m). Contrary to expectations, annual herbs did not increase proportionately with greater aridity. For the mid-elevation belt (3,000–4,000 m) there is a weak, nonsignificant trend for more annual species at 21°–24°S; however, there were proportionately fewer annuals on the desert edge at 21°–24°S and no significant increase again in the upper Andean belt. The difference was exceedingly dramatic along the desert edge at 21°–24°S, where the flora is comprised of seven species of shrubs, two perennial herbs, and one annual (*Philippiamra fastigiata*). In the most stressful climate (aridity confounded by cold stress; 4,000–5,000 m; 21°–24°S) the relative loss of perennial herbs and annuals has been to the extent that the shrub life form becomes dominant for species number. Clear-
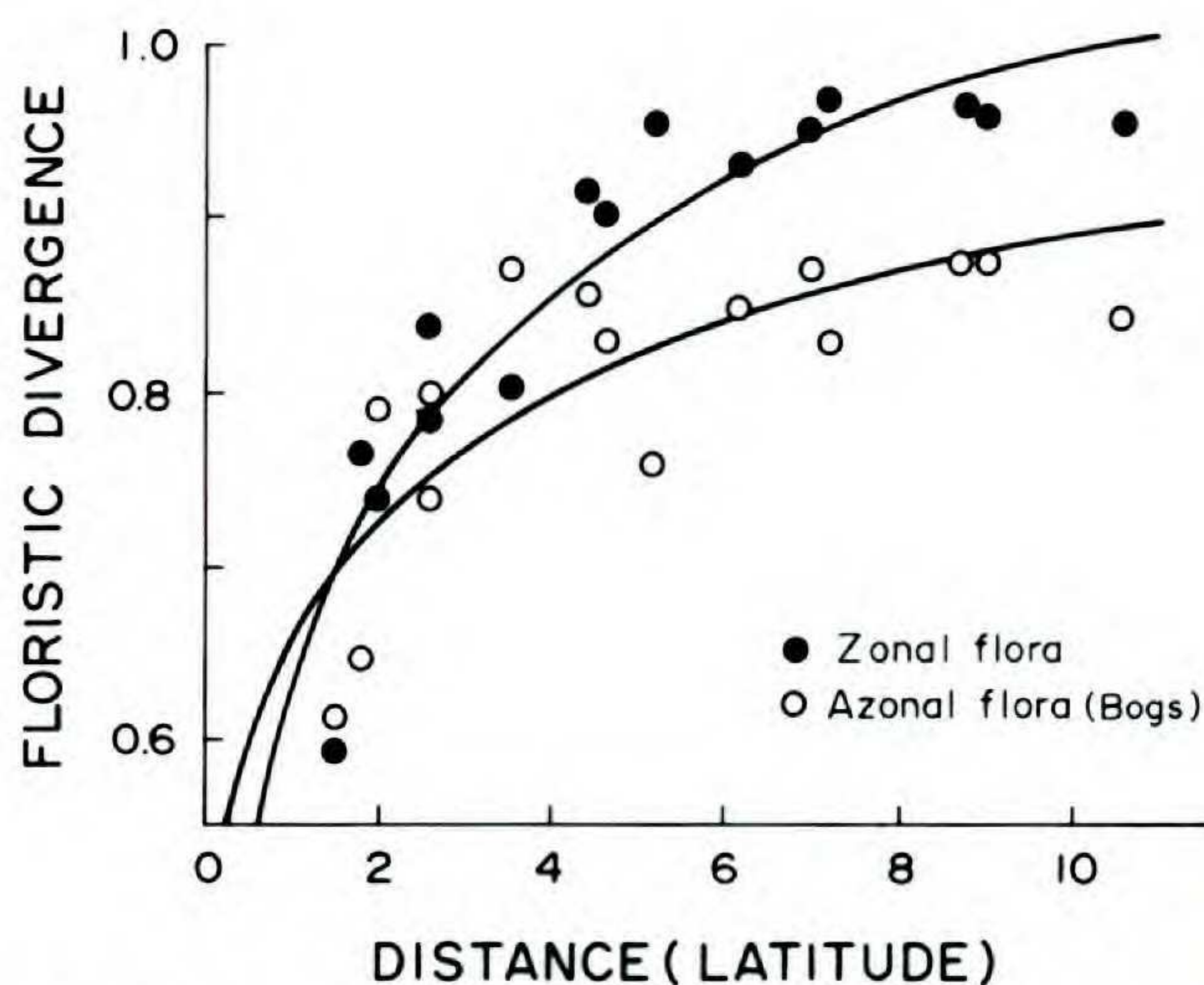

FIGURE 8. *Floristic divergence for all pairs of zonal and azonal (bog) floras between 18° and 28°S in the northern Chilean Andes plotted against the latitudinal distance in degrees separating the pairs of floras compared. Floristic divergence for pairs of floras (A, B) = $(N_A + N_B) / (N_A + N_B + N_C)$, where N_A = number of species confined to area A; N_B = number of species confined to area B; N_C = number of species common to areas A and B.*

ly therefore, in the summer-rainfall area in the northern Andes, the perennial herb life form has been most affected by aridity, followed by the annual herb life form; woody elements have been least affected.

For 26°–28°S (winter rainfall), intermediate proportions of annuals relative to 18°–19° and 21°–24°S were predicted. For the lowermost desert belt (2,000–3,000 m) and mid-elevation belt (3,000–4,000 m), there were no significant differences for any life form when 26°–28°S was compared with 18°–19°S (highest rainfall). For these latitudinal comparisons, however, annuals are more common and perennial herbs less common in the high-elevation (4,000–5,000 m) belt in the summer-rainfall area. When 26°–28°S is compared with 21°–24°S (lowest rainfall), contrary to expectation, annuals did not prove to be in excess in the 21°–24°S area. For the mid-elevation belt (3,000–4,000 m), as is indicated by the nonsignificant difference, the winter-rainfall area has proportionately just as many annual species as the much drier 21°–24°S summer-rainfall region. For the low- and high-elevation belts there are more annuals at 26°–28°S than in the very low rainfall area at 21°–24°S. The higher proportion of annuals at 26°–28°S, where there is winter

snow (and hence much local moisture) in place of rainfall received gradually over the summer months, as at 21°–24°S, again suggests that the annual life form is only adaptive in arid climates up to a certain limit.

To test the robustness of these trends (decrease in perennial life form, increase in annual life form up to a certain level of aridity, dominance of shrub habit in areas of extreme aridity) over a wider sector of the Andes, we compared our data with higher rainfall Andean communities on the eastern side of the Andes (Ruthsatz, 1977) situated immediately opposite the most arid area of the Chilean Andes considered by us (Table 2). Ruthsatz (1977) gave the life forms of over 90% of the species she considered. For 22°–24°S (east) and 18°–19°S (west), most similar in precipitation amounts, there were no significant differences in life forms for any of the three altitudinal levels (comparison D vs. A; Table 2). From east (22°–24°S) to west (21°–24°S) over a very severe rainfall gradient (comparison D vs. B) the life form trends were in very good agreement with those seen previously in north–south comparisons along the western side of the Andes: i.e., perennial herbs are more strongly represented on the wetter eastern side of the Andes and shrubs more strongly represented on the drier western side in the most extreme environments, with annuals increasing only in the more benign mid-elevation belt on the western side. Thus the life-form tendencies revealed on the western side of the northern Andes are also valid on a regional scale.

LIFE FORMS—INTERCONTINENTAL COMPARISONS

Collins et al. (1983) provided life-form data for an altitudinal sequence of floras in the Great Basin in Utah, North America, sharing several floristic elements with the Andes (e.g., *Atriplex*, *Ephedra*) but where rainfall is generally higher. Comparisons for the Andes and Great Basin vegetation belts with similar mean annual temperature (Table 4) reveal the same life-form trends seen across aridity gradients within the Andes, now on an intercontinental scale. For the Andes, with lower precipitation, the woody life form is twice as common and the perennial herb life form only one-half to one-third as common as in the Great Basin. Annual herbs are in excess in the mid-elevation belt on the western side of the Andes compared with Mt. Nebo. However, despite the much lower rainfall along the desert margin and in the high-elevation belt compared with Arches and Bald Mountain, respectively, there is no proportional increase for annuals in these harshest climates in the Andes. This once again emphasizes that annuals increase with aridity but that there is a critical point at which the woody habit becomes relatively more appropriate for arid climates.

Most surprisingly, as the Arches vs. 2,000–3,000 m (22°–24°S, eastern Andes) shows, woody species continue to be in excess and perennials in deficit in the Andes when annual precipitation is relatively similar. This indicates that the northern Andes exhibit a generalized excess in woody species over the Great Basin beyond local trends in the latter for increased frequency of woody species with habitat harshness.

COMMUNITY DIVERSITY PATTERNS

In harsh arid habitats, as was argued earlier, relatively higher community diversity levels, as seen at the early stages of primary succession, are to be expected as a permanent community feature in spite of overall low species richness.

In the Andes, regressions of exp H' and $1/\lambda$ on species richness and cover show (Figs. 9, 10) that harsh environmental conditions, on a biogeographical scale, lead to an overall trend for loss of diversity. Thus the primary succession analogy proposed is not entirely supported. Over each gradient (Fig. 11) diversity peaks at mid elevations, where conditions are neither the coldest nor the most arid, as was seen for species richness and cover; however, decreases in diversity are not commensurate with reductions in species richness. This phenomenon is more easily appre-

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TABLE 4. *Statistical comparisons (G-tests) for life forms in the flora of the northern Andes (west and east sides) and the Great Basin, Utah. Comparisons are made for elevational levels with the closest mean annual temperatures. Data for the Andean areas are those in Table 2. Data for the Great Basin taken from Collins et al. (1983).*

Great Basin, Utah		G-test (Utah vs. Western Side of Andes)		G-test (Utah vs. Eastern Side of Andes)
		18–19°S (2,000–3,000 m)	21–24°S (2,000–3,000 m)	22–24°S (2,000–3,000 m)
Arches (1,200 m)				
(13.5°C; 217 mm)[1]		68 mm	6 mm	200 mm
Shrubs & trees	18.32%	12.59*** (Andes[2])	NA[4]	17.66*** (Andes)
Perennial herbs	62.73%	11.80*** (Utah)	NA	12.34*** (Utah)
Annual herbs	18.94%	3.09; NS[3]	NA	1.20; NS
(322 spp.)				
Mt. Nebo (2,500 m)				
(9.4°C; 641 mm)		153 mm	30 mm	249 mm
Shrubs & trees	12.98%	37.88*** (Andes)	25.48*** (Andes)	48.12*** (Andes)
Perennial herbs	76.51%	53.04*** (Utah)	56.58*** (Utah)	44.08*** (Utah)
Annual herbs	10.51%	5.90* (Andes)	17.82*** (Andes)	0.76; NS
(647 spp.)				
Bald Mt. (3,200 m)				
(−2.4°C; 1,028 mm)		266 mm	97 mm	330 mm
Shrubs & trees	8.96%	6.38* (Andes)	26.48*** (Andes)	5.85* (Andes)
Perennial herbs	85.82%	5.86* (Utah)	32.81*** (Utah)	6.50* (Utah)
Annual herbs	5.22%	1.10; NS	3.19; NS	0.29; NS
(134 spp.)				

[1] Mean annual temperature and mean annual precipitation.
[2] Area for which life form is proportionately better represented.
[3] Significance levels for G-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; NS = not significant.
[4] G-test not applicable.

ciated in Figure 12, in which diversity and species richness are compared for equivalent elevations from the wetter 18°S to the drier 24°S. At 3,000–3,500 m and 3,500–4,000 m, where conditions are more favorable on each transect, there are significant reductions in diversity as aridity increases; however, they are shallower than for species richness. As higher elevations doubly stressed by aridity and cold temperature are reached, there is no significant difference in diversity from 18° to 24°S in spite of considerable reduction in species richness. Thus, in the sense that community diversity is maintained relatively high in the face of large losses in species richness, the diversity trends seen in the most arid areas of the northern Andes are indeed analogous to a primary succession situation.

The more gradual loss of diversity relative to species richness may be related to the relative contribution of each life form and the presence of far more rare species in the relatively benign areas. In the most productive environments (18°S), one life form typically stands out as strongly dominant. Moreover, within that life form a few fairly abundant species tend to be accompanied by large numbers of relatively rare species. At mid elevations at 18°S, for example, in spite of the fact that *perennial herbs* are well represented in numbers of species (see section on life forms), the woody life form is more abundant than the herbaceous life forms (which can persist in low densities because of the relatively benign conditions). Within the shrub guild, close coexistence, moreover, seems to have precipitated fairly strong dominance hierarchies as seen in great abundance of such
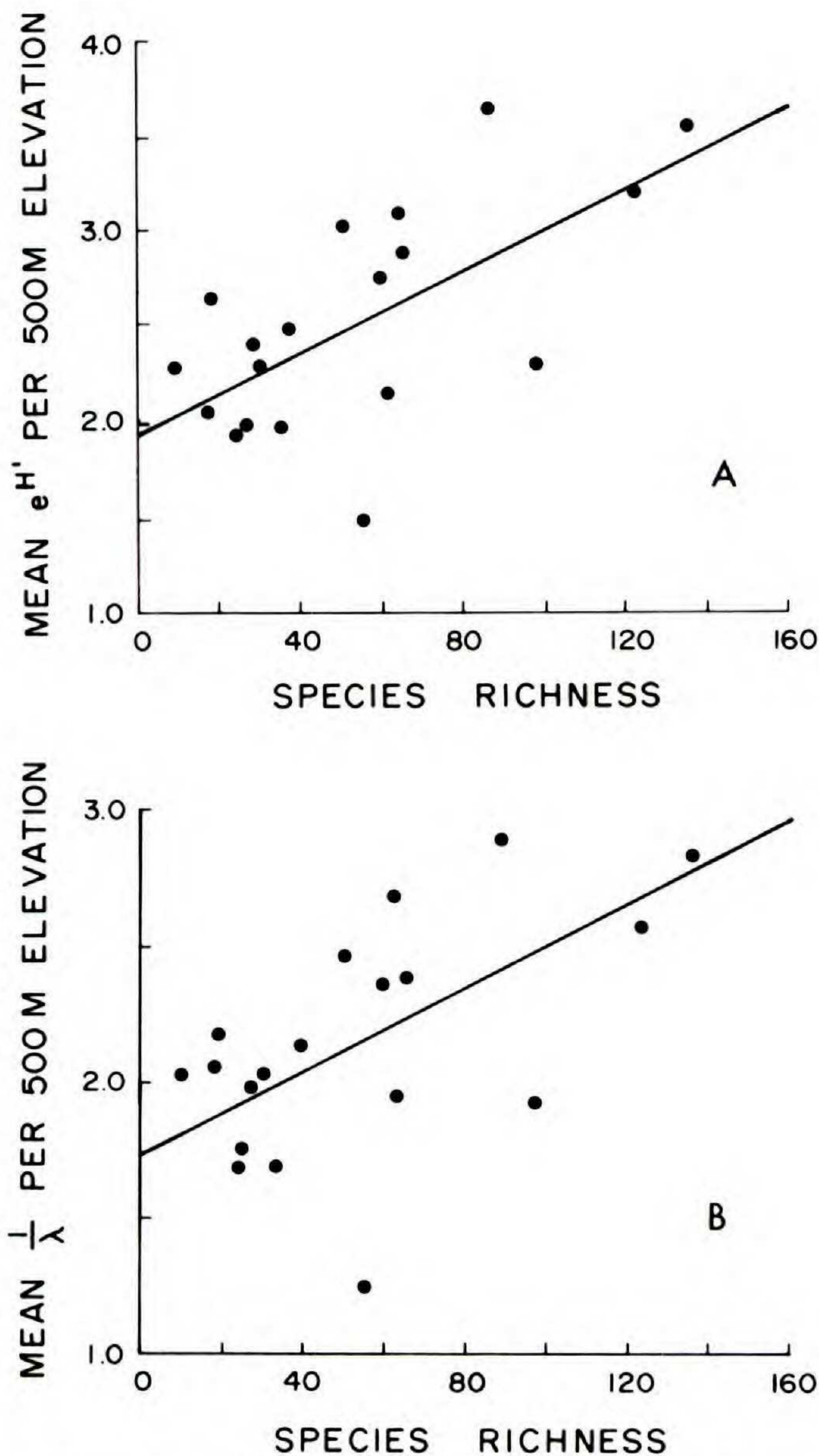
FIGURE 9. *Linear regressions of diversity on number of species (species richness).—A. exp* H′ *vs. species richness (*y = 0.010x + 1.96*; F = 11.511; d.f. = 17; P = 0.003, where* y = exp H′ *and* x = *species richness).—B.* 1/λ *vs. species richness (*y = 0.019 + 0.007x + 1.78*; F = 2.811; d.f. = 17; P = 0.01, where* y = 1/λ *and* x = *species richness). Points on graphs correspond to 500-m elevational intervals on the four summer-rainfall transects.*

species as *Fabiana densa, Baccharis boliviensis, Ephedra breana,* and *Diphlostephium meyenii.* From 4,500 to 5,000 m at 18°S, bunch grasses become strongly dominant over shrubs, and again there are few strongly dominant species (*Festuca orthophylla, Poa* sp.). In the less productive environments at 21°–24°S, in contrast, for the high elevations in particular, abundance levels for shrubs and herbaceous species are probably more equitable, in spite of the fact that there are relatively fewer species of perennial herbs. These last considerations are based on
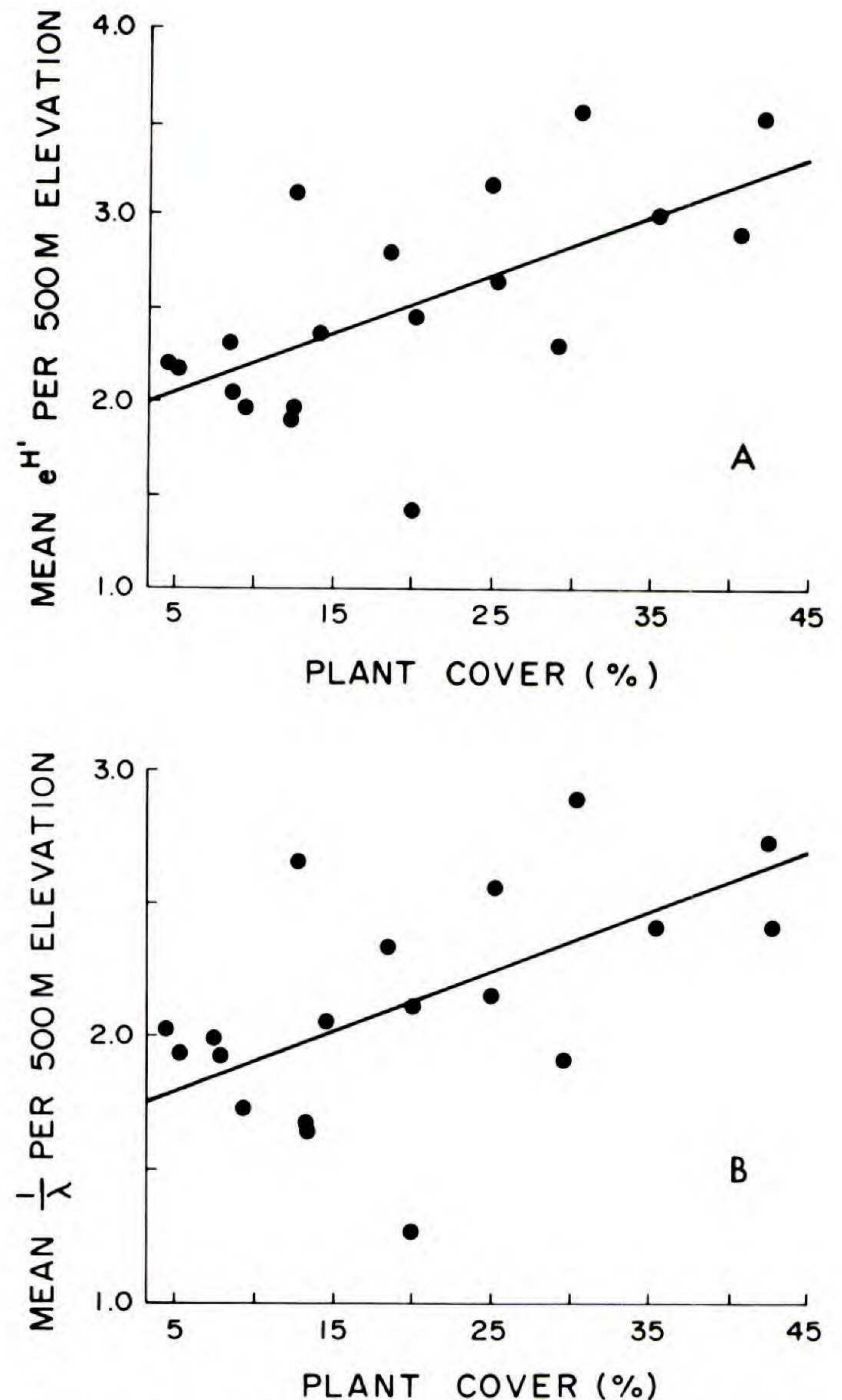

FIGURE 10. *Linear regressions of diversity on plant cover (% ground vegetated).—A. exp* H′ *vs. plant cover (*y = 0.032x + 1.904*; F = 12.06; d.f. = 17; P = 0.005, where* y = exp H′ *and* x = *plant cover).—B.* 1/λ *vs. plant cover (*y = 0.019x + 1.762*; F = 7.06; d.f. = 17; P = 0.05, where* y = 1/λ *and* x = *plant cover). Points on graphs correspond to 500-m elevational intervals on the four summer-rainfall transects.*

direct observation; much analytical work is still required to characterize dominance relations in the Andean flora.

DISCUSSION

Patterns of plant diversity have been described for an area that underwent dramatic environmental upheavals in the Pleistocene and which acquired its present extreme arid character over a relatively short period.

The effects of aridity on species richness in the northern Andes clearly have been severe. The 769 species for all transects are believed to include about 75% of all species
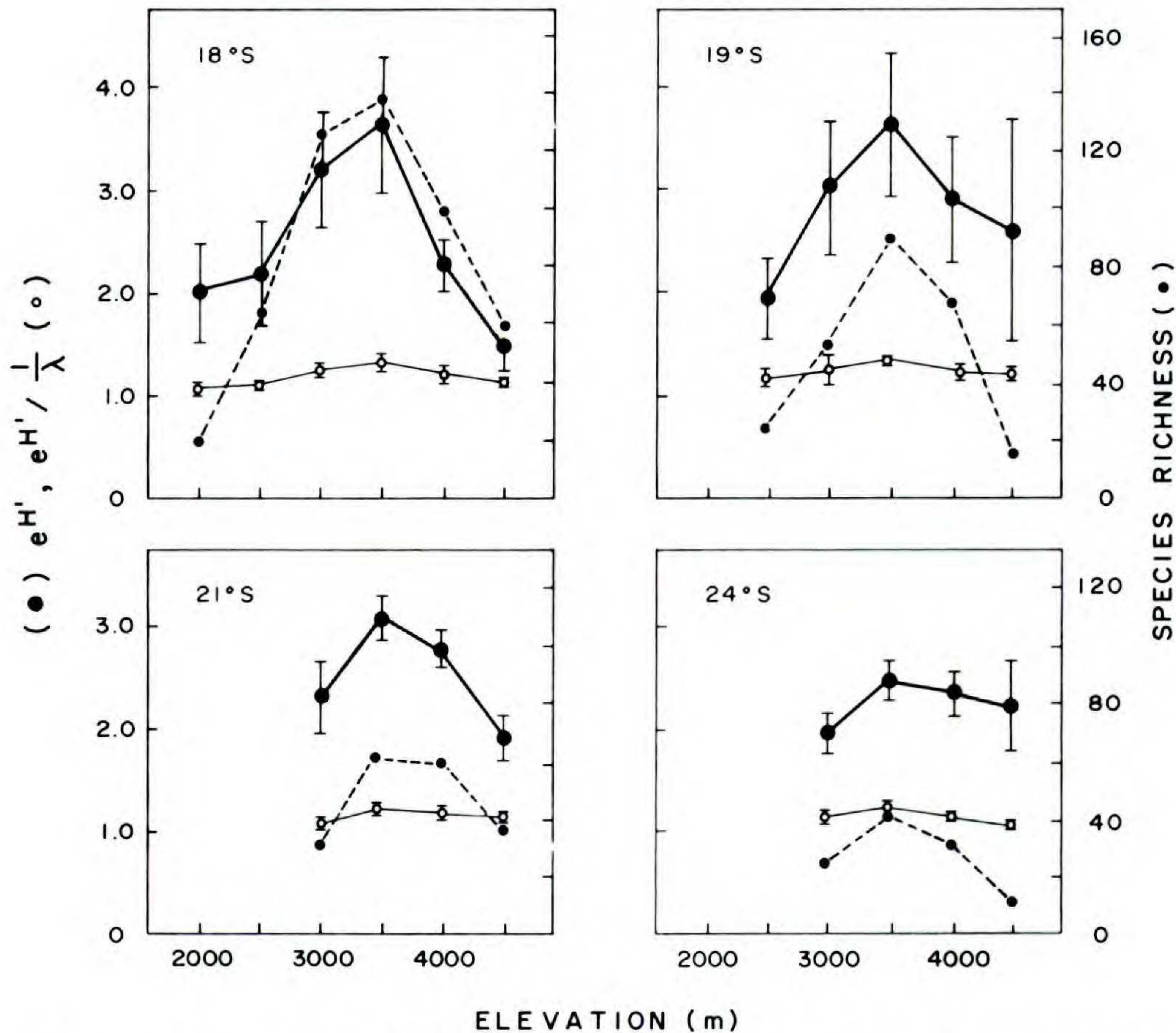
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FIGURE 11. Mean exp H', exp H'/(1/λ), and species richness vs. elevation at different latitudes in the northern Chilean Andes. Lack of variation in exp H'/(1/λ) indicates that diversity trends resulting from application of 1/λ as a diversity index are similar to those obtained using exp H'. Vertical bars are 95% confidence intervals for the means.

from 1,500 m to the upper vegetation limit from 17°S to 28°S. This leads to an estimate of under 1,000 species per 10° latitude or the equivalent of less than one-fifth of the total Chilean flora (Marticorena & Quezada, 1985). This is only one-sixth more species present over 1° of latitude from 3,500 to 5,000 m in Parque Nacional Huascaran (8°S) in the northern Peruvian Andes (estimated by David Smith, pers. comm., to have 660 species). It is only just over three times the number above tree line (309 species) at 33°S (Arroyo et al., 1983) for an area similar to that sampled in the individual northern transects and in the paramos of Colombia (4°N; Rangel et al., 1983), where 321 species occur above tree line on an area covering much less than 1° of latitude. The Andes of Jujuy in northwestern Argentina (22°–24°S) immediately across the main divide, where it was seen that rainfall is much higher, support 622 species (Ruthsatz, 1977), in contrast to only 199 at 21° and 24°S on the Chilean side.

Areas least affected by aridity and cold temperature proved to be richest in species. Such areas also exhibit high community diversity. Highly stressed areas with low species richness, nevertheless, are relatively robust for community diversity. Any seasonal variation in annual growth, as along the desert edge, could greatly affect community diversity estimates. Revisits to the Andean highlands in from Arica (18°S) in a very wet year subsequent to vegetation sampling leave little doubt that annual cover at lower elevations there fluctuates widely. However, the trends above 4,000 m, where there are very few species of annuals, are unambiguous.

Maintenance of relatively high local levels of community diversity in the most arid areas will probably turn out to be the result of lowered dominance levels in the drier areas. Thus aridity, the very feature driving lowered species richness in the Andes from the outset, probably eventually reduces the rate at which local diversity declines. In this sense the not
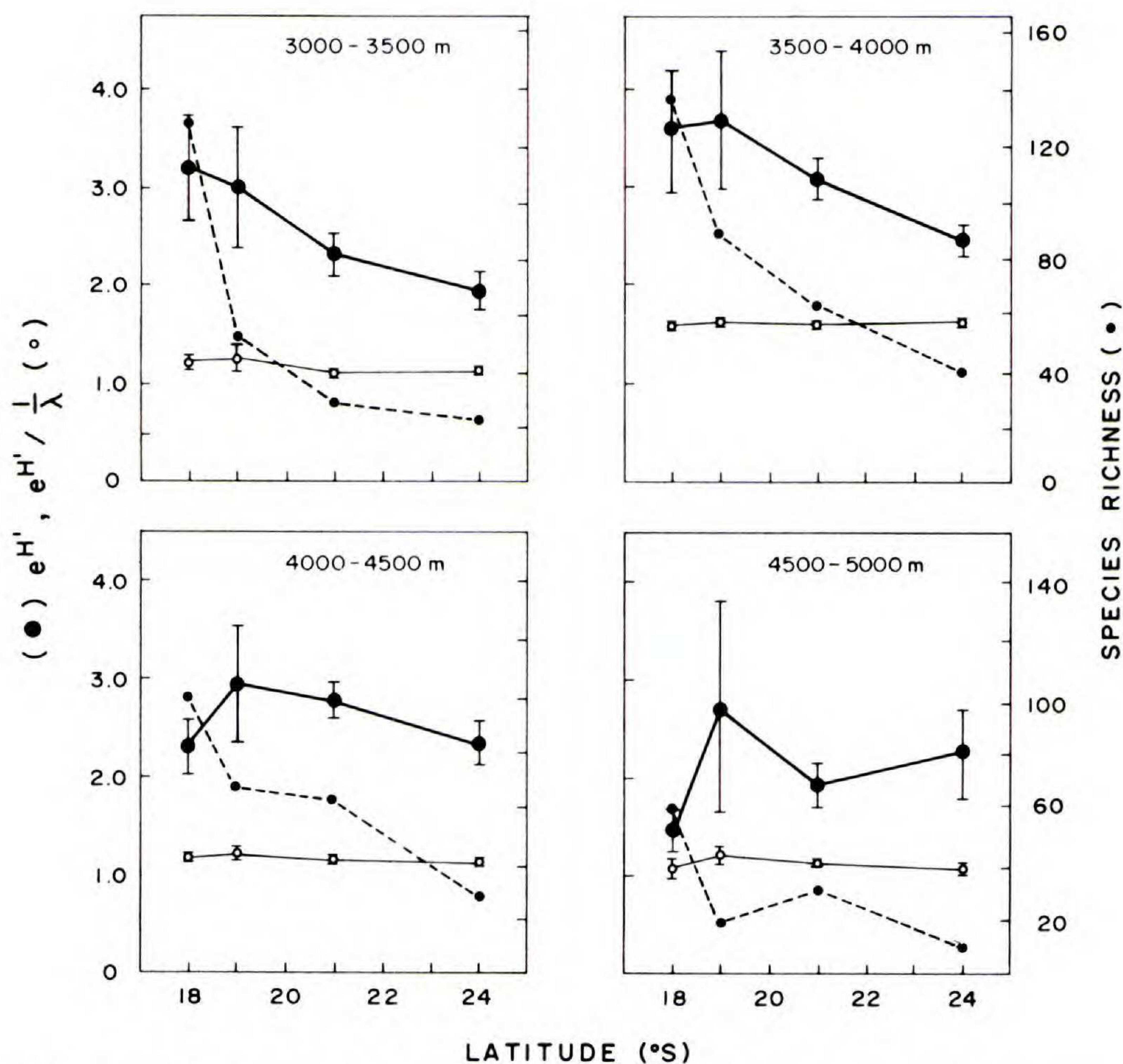
FIGURE 12. *Mean exp* H', *exp* H' / (1/λ), *and species richness vs. latitude from 18°S (maximum precipitation) to 24°S (minimum precipitation). Lack of variation in exp* H' / (1/λ) *indicates that diversity trends resulting from application of 1/λ as a diversity index are similar to those obtained using exp* H'. *Vertical bars are 95% confidence intervals for the means.*

strongly exponential drops in species richness with aridity should be recalled. They seem to indicate that loss of species richness has been counteracted to some extent. The life-form changes we have demonstrated must also be important here; however, it is far too early to sort out the relative contributions of different factors against species richness loss.

Stress-tolerant (e.g., annual life form) and stress-resistant (e.g., shrub life form) strategies are often considered as hierachically equivalent alternatives for harsh environments. Our results suggest that woody species gain prominence over annuals on the harshest of the Andean habitats. Significantly, moreover, some of the most successful "perennial herbs" from the driest areas of the Andes (e.g., *Sisymbrium philippianum, S. lanatum, Tarasa operculata*) have semiwoody stems. Thus the trend towards woodiness goes beyond simple reshuffling of the taxa present

and is probably being actively selected for in some individual taxa.

Woody species are probably best adapted to extreme aridity through a combination of ecophysiological and demographic features. Root/shoot ratios for warm-desert species are usually around one, and there is relatively little vertical root growth (Barbour, 1981). In contrast, root/shoot ratios in excess of four have been reported for shrubs in cold North American and Eurasian deserts (Caldwell, 1985). This suggests that for cold arid areas, where growth is relatively slow, large long-lived species might be favored by being able to produce larger root systems that would reach deep into the soil over a prolonged growth season. Soils in the northern Chilean Andes are largely volcanic, hence surface water is probably always limited. Further, in the driest areas of the summer-precipitation zone, rain comes in light morning showers

and is never abundant at any one time. We suspect that this factor favors shrubs in the driest areas and, as was mentioned earlier, explains why annuals are generally less frequent in the summer-rainfall zone.

Because they tend to be long-lived, woody species require less frequent establishment events (Schaffer & Gadgil, 1975). This should be highly advantageous in habitats where seed germination and seedling establishment are precarious, as is the case with strongly arid climates. Seed production is not only a function of pollination success and of resources allocated to reproduction, but also of the probability of an adult reaching reproductive maturity and its physiological state at that stage. Woody-stemmed shrubs are more likely to reach reproductive maturity than soft-stemmed herbs because of their greater resistance to drought. In spite of the fundamental nature of the question, as far as we know, to date there have been no attempts to appraise the relative importance of the physiological and demographic features of woody species in harsh environments.

The greater representation of woody species in the northern Andes might reflect the Andes being located some ten degrees of latitude closer to the equator than is the Great Basin. The floristic matrix out of which the Andean flora evolved, as a result, probably possessed a higher percentage of woody elements initially. Fossil floras for the Great Basin (Axelrod, 1979a, 1983) and as far south as the Chihuahuan desert (Wells & Woodcock, 1985) show North American desert floras emerging out of open woodland with many herbaceous elements. The radical climatic changes at each glacial/interglacial interface in the Andes should have further impoverished the herbaceous flora. These historical factors, apart from effects of present climatic characteristics, should have produced a gradual accumulation of woody elements in the northern Andes.

Heavy grazing in the Andes (alpaca, llama) has possibly influenced the broad intercontinental differences in life form. Interestingly,

areas of the northern Andes in which woody species are most strongly represented today are least affected by grazing (e.g., 21°–24°S), while those with well-developed herbaceous floras can be heavily grazed (north of 19°S). Very plausibly, climatic and biotic factors have acted in concert to produce the intercontinental differences in life form.

Emphasis on the long-lived, woody life form, as seen in harsh environments in the northern Chilean Andes, is also a feature of tropical and other forests developed in abiotically benign conditions. For the tropics in particular, longevity is usually seen as a correlate of large body size resulting from selection for competition for light (Grime, 1979). Much woodiness in the tropics could equally bear relation to the demographic advantages of being long-lived, as was suggested for abiotically harsh habitats. In the tropics, seed predation (Ramirez & Arroyo, 1987) and fungal infections (Ramirez & Arroyo, 1984) can significantly lower successful seed germination. Additionally, juvenile mortality can be high due to strong intra- and interspecific competition for light and nutrients (Connell et al., 1984) and leaf predation (Clark & Clark, 1985). These features have direct parallels in the extremely arid Andean ecosystem, the difference being that in the tropics they are mediated through the biotic environment rather than the abiotic environment. Grime (1979) recognized that "stress" in productive environments arises mainly through competitive depletion of resources (the biotic environment). Yet he perhaps placed undue emphasis on longevity in tropical ecosystems as being a result of selection for direct competitive ability without paying much attention to the demographic advantages. As in arid environments, the role of longevity for tropical forests needs more critical assessment.

Diversity patterns in the kinds of "abiotically" harsh environments we studied and in "biotically harsh" tropical forest communities might also show convergent trends. Many tropical forests lack clear dominants—dominance is probably less well developed in the

most arid environments we studied. Lack of dominance in tropical forests has been seen as an effect of reduced opportunities for co-evolution resulting from low interspecific connectance sensu Pimm (1984) (Connell, 1980), or in Buckley's (1983) words, "in diverse, well-mixed communities individuals cannot predict their neighbours." Hubbell & Foster (1986) proposed a similar but not identical hypothesis: individual species are seen to reflect the temporal and spatial average of biotic selective conditions created by ever changing and diffuse competitors, leading to guilds of functionally equivalent generalists. Sustained biotic interactions are also seen to be limited in very arid environments. Wetter deserts like the Mohave and Sonoran provide some evidence of root competition between widely spaced individuals (Yeaton & Cody, 1976; Phillips & MacMahon, 1981). Gulmon et al. (1979), by contrast, concluded that limited opportunities for establishment lead to little competition between individuals of the long-lived *Copiapoa* (Cactaceae) in the Chilean coastal desert at 25°S, where ca. 25 mm of rain falls annually. This is tantamount to low connectance, the abiotic environment assuming the role of the biotic environment in a tropical forest.

We suspect that a suite of common features will be revealed for these two kinds of "harsh" environments for the organisms that inhabit them. Convergence could be expected in breeding system (e.g., levels of sexual dimorphism), seed size, and sexual selection. Some of these possibilities are presently being studied by us in cold alpine habitats in the Chilean Patagonia (e.g., Arroyo & Squeo, 1987).

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